49. Some Observations on Pattern-Blending with reference to Obliterative Shading and Concealment of Outline.

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(Text-figures 1–5.)

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This paper endeavours to show that the patterns found on animals may in many cases be of use in concealment after they have become blended with distance, and that the patterns of many animals are not intended to represent pictures of their backgrounds, but are aids to concealment only after blending.

Distance at which Blending takes Place.

If a surface of black and white squares or of black and white lines, or black and white spotted surfaces be examined from successively increasing distances, a point will be reached where the

Text-figure 1.

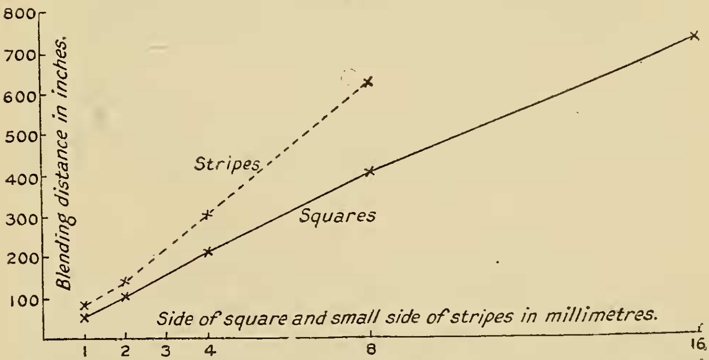


Diagram showing blending distances. Experimental conditions as in text-fig. 5, *1*.

pattern can no longer be seen but is replaced by an even grey tone. The distance at which this change takes place was found to depend on the size of the black and white areas. The diagram (text-fig. 1) indicates the distances at which blending takes place in

* Communicated by the Secretary.

the case of alternate black and white squares and stripes under the experimental conditions stated.

Further experiments showed that the blending distance of different shapes depends upon the relative concentration of the black and white areas, the more concentrated the greater the blending distance. If, for instance, a checkered surface composed of squares of 2 square millimetres be compared with a surface composed of black and white oblongs of 1 multiplied by 4 mm. or ·5 multiplied by 8 mm. or ·025 by 16 mm., as regards the blending distance, it will be found that the distance is greatest for the squares and least for the narrowest oblongs. On comparing squares with other figures in this respect, for instance, with circles or triangles, it was found that the blending distance was related to the concentration of the various shapes.

The Surface which Results after Blending.

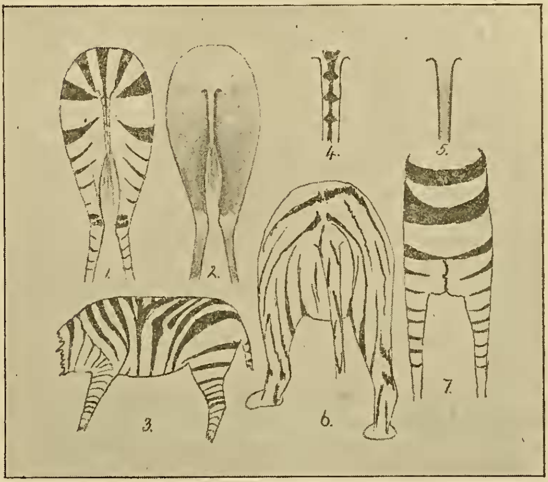
If a patterned surface of black and white be gradually approached from a distance, the surface which at first appeared of a perfectly even grey tone will, at a certain point, become granular, and a very short distance in front of this the pattern will suddenly shine forth clear and defined.

By varying the relative proportion of black to white in the pattern, all tones of grey can be produced when the pattern is blended. It is thus possible to match a given grey surface by means of black and white pattern, and also possible to reproduce a graded surface of grey: text-fig. 3, *1*, shows without any description how this can be done. If these copies of greys with patterns be fixed to solid figures such as a cylinder and be then examined, it will be found that after blending, the copies are undisturbed. It follows that the obliterative shading so commonly seen on animals and consisting of low tones where the light strikes, high tones in the shadows, and intermediate tones between the two, could be reproduced by means of pattern. Search has therefore been made amongst animals to discover whether this method exists.

Some Examples of Animals which appear to show Obliterative Shading by means of Pattern-Blending.

Grant's Zebra (*Equus burchelli granti*).—This animal's coat is coloured black and white, black stripes on a white background: the background, unlike that of the vast majority of animals, presents no obliterative shading, it has the same tone throughout; the stripes are somewhat darker on the back than they are below. On referring to text-fig. 2, *3*, it can be seen that on the dorsal surface of the animal and on those parts of the body where the light strikes, the stripes are broad, whereas on those parts which under natural conditions would be in shadow, the stripes are narrow: further, on those areas which would be more or less evenly lit, as for instance the vertical surfaces of the legs and sides of the face, the stripes maintain a more or less constant width. From what has been observed under experimental conditions as regards pattern-blending, it is obvious that, if one considers only the trunk of this animal, the varying widths of the stripes after blending must produce a condition of grey similar exactly to obliterative shading as seen, for instance, in the ass.

Text-figure 2.



1. Grant's Zebra (*Equus burchelli granti*), hind view.
2. The same view: stripes omitted: showing chief shadows under top lighting.
3. Lateral view of same animal.
4. Hind view of base ot tail, showing pattern.
5. Hind view of base of tail, pattern omitted, showing shading as in 2.
6. Hind view of Tiger (*Felis tigris*), showing pattern.
7. Front view of Grant's Zebra, showing pattern.

Amongst big-game hunters there is a difference of opinion as to whether this animal is easily seen or not, under natural conditions. It appears that this difference of opinion is largely due to the district in which the hunter has observed these animals. In some districts the zebra is relatively tame and the hunter can frequently approach to within the blending distance of the pattern, which has been variously estimated, according to the lighting: under these conditions the zebra will of course appear a very conspicuous animal. On the other hand, in those districts where near approach cannot be gained on account of the open nature of the country or wildness of the animal, the hunter will look upon the zebra as one of the most difficult wild animals to pick up.

Of the zebras, *E. burchelli* presents between the stripes considerable obliterative shading, as well as faint stripes of buff. *E. grevyi* also has some obliterative shading, *E. zebra* very little, and *E. burchelli granti* none at all. Complete absence is, however, not uncommonly seen in all the species.

Thayer, in 'Concealing Coloration in the Animal Kingdom,' looks upon the striped coat of this animal as an obliterative picture-pattern of rank grasses and tree-stems: it is noteworthy that he makes no mention of the absence of obliterative shading, which he elsewhere insists always forms the canvas for picture-painting. If, however, examination be made of the pattern to be seen on viewing a zebra from behind (see text-fig. 2, *1.*), it is at once evident that this does not represent a picture-painting of reeds, herbage or trees. On the other hand, it illustrates in a remarkable way obliterative shading by means of pattern. Text-fig. 2, *2*, is a modelled drawing of the same view with the stripes omitted, the lighting being from above, and shows the major shadows which are cast. On comparing these two figures it can be seen that in the high lights, the stripes are broad, and that as one passes into the shadows, they fade away: where the high light strikes the hocks the bands are broad, whereas below the hocks where the leg is in the shadow, the stripes are narrow. The striping on the tail even falls into line, as shown in text-fig. 2, *4*, *5*.

The Guineafowl (*Numida meleagris*).—This bird illustrates obliterative shading by means of white spots on an even blue-grey background (text-fig. 3, *1*, bottom right-hand square). On the back the white spots are small, but become larger as one passes to the ventral aspect, where they are four times the diameter of those on the back. In some species the wings are covered with a series of short white bars, narrow on the back and broader below, as the wing lies covering the body during rest. These markings on the bird blend at a comparatively short distance; within the blending distance the bird appears conspicuous, beyond, difficult to see. The bird lives in open country, and there does not appear to be anything in its surroundings which this pattern emulates.

The Cheetah (*Cynælurus jubatus*).—The pattern, as shown in text-fig. 3, *1*, bottom left-hand square, consists of black spots on a pale fawn background: the background presents either no obliterative shading or very slight; the spots are close together on the back, gradually becoming more distant towards the ventral surface, which is hidden by a fringe of long hairs projecting downwards from the flank.

The Serval (*Felis serval*) presents a similar pattern to the Cheetah except that in the dorsal region, spots are replaced by short bars. This kind of pattern is commonly seen in the Civets.

The Jaguar (*Felis onca*).—Here the pattern is laid on a background presenting very little obliterative shading : on the back are closely placed black spots ; as the ventral surface is approached the spots are seen to contain a central light brown area which gradually increases in size, whilst the surrounding dark ring diminishes and on the ventral surface becomes broken up into a number of separate spots irregularly arranged around the central area. This central area is always somewhat darker than the background and usually contains a small central black spot. Viewed as a whole this rather complicated pattern (see text-fig. 3, *17*) shows a decreasing quantity of black from above, downwards, and when blended at distance will produce a graded tone similar to obliterative shading. A similar pattern is found in the Ocelot (*F. pardalis*) and in several varieties of the Leopard, where it is often associated with an entire absence of obliterative shading.

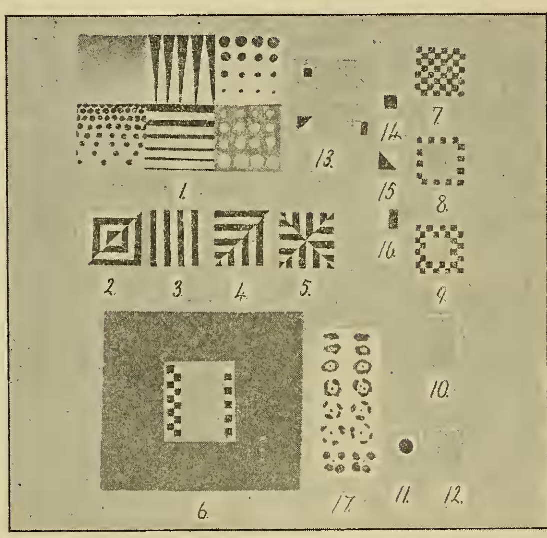
These patterns found in the genus *Felis* have been considered to be picture-paintings of a checkered background, for instance, leaf-shadows on bare ground ; but the extreme regularity of these patterns is so unlike the very irregular nature of such backgrounds and so unlike the patterns which undoubtedly *do* simulate these backgrounds, that this deduction does not appear to be well founded ; especially as these patterns blend at a comparatively short distance, probably within the charging length of the cat : and lastly, several of these animals inhabit open country.

However, apart from this consideration, the facts remain that these patterns will produce after blending obliterative shading, which is otherwise not presented ; and these patterns must in this respect be powerful aids in concealment.

Sufficient examples have now been given to illustrate that this method of concealment is by no means uncommonly utilised. Black and white has been chiefly dealt with, but any colour can be produced by the blending of patterns consisting of two or more colours : examples of this are not difficult to find, for instance brown is often produced by the blending of buff and black.

Experiments were carried out to discover whether this method of coloration had any advantage over an unpatterned one. If a grey disc be examined in front of a series of backgrounds varying from black to white, a particular background will be found against which the grey disc is invisible, this being of course that background which is of an exactly similar tone to the disc : against the other backgrounds the disc will be visible at varying distances. If the results so obtained be compared with those obtained when a disc of black and white squares, which after blending produce the same tone of grey as the original disc, is substituted, it is found that the checkered disc possesses no advantage as regards the distances at which it can be seen, over the plain disc. There is, however, an exception : against the background on which the plain disc is invisible, the checkered disc is of course visible within blending distance, and against backgrounds closely similar to this background the checkered disc is at a disadvantage as regards invisibility. Over a long series of experiments there was some indication that against other backgrounds the checkered disc was slightly less visible, the measure being the greatest distance at which the discs could be seen; but although great care was taken with the constants of the experiment, the differences were too small and the experimental error too large, to justify a definite conclusion, particularly as the appearance of the checkered disc after blending was remarkably different from that of the plain disc. When the plain disc was visible, its outline was seen to be sharp, so that its shape could easily be recognised, but with the

Text-figure 3.



Examples of obliterative shading by means of pattern-blending.

checkered disc the outline was remarkably indistinct, so that it was frequently impossible to tell whether a square, circle or equilateral triangle had been placed against the background. Experiments were carried out in order to determine the factors controlling this obscuring of form. Four squares were prepared as shown in text-fig. 3, *2–5*: as can be seen, these squares consist of black and white areas of equal proportions. In fig. *3* the areas are interrupted along the two opposite margins, in fig. *4* along the two adjacent margins, in fig. *5* along all four edges, and in fig. *2* there is no interruption at the margins. These squares were examined under different conditions of lighting and against different toned backgrounds, and it was found that on all occasions marginal indistinctness after pattern-blending occurred where the black and white areas were interrupted at the edges; for instance, fig. *2* appeared as a grey square whilst fig. *5* showed an ill-defined grey area fading into the background. It was noted that when the background was near in tone to the squares after blending of the pattern, this obscuring effect was most marked: when the background was far removed in tone, for instance was black, or white, very little obscuring was noticeable. Other experiments showed that the greater the width of the black and white areas passing out at the margin, the greater the obscuring effect after pattern-blending.

One is now in a position to conclude that the method of obliterative shading by pattern-blending, as seen for instance in the Zebra, if it does not possess an advantage over the usual method as regards visibility, as measured by the distance at which the object is visible, nevertheless would seem to have a decided advantage in that the contour or silhouette of the animal against backgrounds approaching it in similarity, is made blurred rather than sharp. It is noteworthy that the stripes of the Zebra everywhere pass out at the margins (see text-fig. 2, *1*, *3*, and *7*).

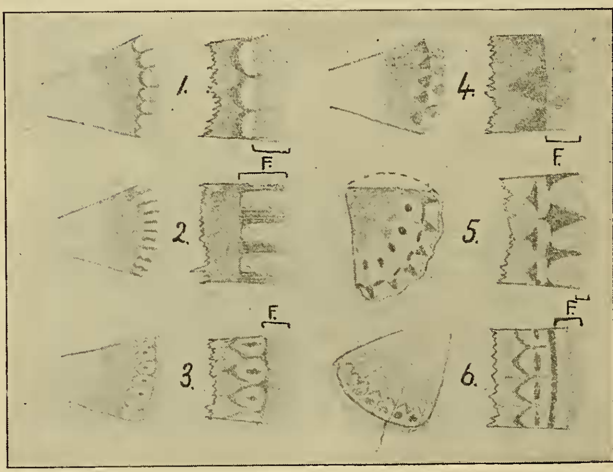
Referring to the possibility of the Zebra's stripes being pictures of reeds in high light and shadow, as has been suggested by Thayer, it is noteworthy that the black stripes decrease in breadth from above, down, which is contrary to expectation and to what actually is found among other animals. Thayer has pointed out that the markings on the backs of animals are usually smaller than those on the ventral aspect, because they represent objects in the landscape more distant: they depict the foreshortening of the ground. If reeds are painted on the zebra's back, one would at least have expected the stripes to be of equal width.

The Tiger presents an excellent example of reed-painting: on a coat showing well-marked obliterative shading, dark stripes are to be seen, they are irregularly distributed, they for the most part increase in width from above, down, and on the belly they terminate in a large dark mass which, curiously enough, often shows a small white centre (compare text-fig. 2, *1* with text-fig. 2, *6*).

Examples of outline-masking by means of pattern-blending at the margins are very commonly seen amongst Lepidoptera, but before considering instances, some experiments must be referred to. If one takes two flat surfaces, one an even dark grey and the other an even light grey, and brings them in apposition as shown in text-fig. 3, *6*, the junction will appear sharp, no matter how viewed. If now, at the junction a narrow band of black and white squares, which after blending will have the same tone as the light square, be interposed, see text-fig. 3, *6*, it will be found that the junction no longer remains sharp; if the outer square be replaced by areas of different tones varying from light grey to very dark grey, the same result will be seen. It is easy to see that, supposing the central square was an insect and that the different tones placed outside were the various backgrounds against which it would be likely to be seen, then the possession of a checkered margin would be a great aid towards its concealment.

To further test this property of an interrupted margin, squares were made as shown in text-fig. 3, *7–10*: these squares were made so that after pattern-blending they all appeared of the same tone. They were examined against a series of backgrounds and it was found that, whereas *10* remained for the most part sharp, the others showed blurred outlines; the blurring effect in the case of square *7* was not appreciably different from that of *8* and *9*. It appears therefore that a comparatively narrow broken margin is effective.

Text-figure 4.



Examples of marginal patterns: F=fringe of scales projecting from wing-margin.

1. Dingy Skipper, *Hesperia tages* ♀, dorsal surface of anterior wing.

2. Grizzled Skipper, *H. malvæ* ♀, dorsal surface of anterior wing: pattern confined to fringe.

3. Common Blue, *Lycæna icarus* ♂, ventral surface of anterior wing: pattern of marginal eye-spots.

4. Chalk-hill Blue, *L. corydon* ♀, dorsal surface of anterior wing: pattern chiefly confined to fringe.

5. Painted Lady, *Pyrameis cardui*, dorsal surface of posterior wing.

6. Long-tailed Blue, *L. bætica*, ventral surface of posterior wing: pattern at some distance from margin.

A few examples of this mode of concealment are given in text-fig. 4: it may be mentioned that outline-masking in insects is also brought about by scalloping of the margin and by a fringing of projecting scales; other methods are utilised, but these two are specially mentioned as they enter the chosen examples.

Examination of the wings of insects showed that this marginal pattern is often a short distance from the extreme edge; experiments were therefore carried out to discover at what distance the marginal pattern would be effective. A grey square (text-fig. 3, *6*) was examined against varying backgrounds with the checkered margins (equal in tone after blending) placed at varying distances opposite free margins, as shown in the figure. It was found that the marginal blurring, produced by the checkered patterns, was effective when they were placed a very short distance from the margin. Up to the width of the squares used some effect was noticeable, but was much more marked when the distance was produced to one half or a quarter of this. The single row of squares appeared to be almost as effective as the double; attempts were made to obtain more definite results, but in the absence of some method for estimating the amount of blurring, this was found to be impossible. Text-fig. 4, *6*, is an example in which the marginal pattern is separated a short distance from the free edge.

As eye-spots are frequently to be seen near the margins of the wings in Lepidoptera, it was thought that they might play some part in concealment of form by means of outline-blurring. A few experiments were carried out to discover whether this be so or not. In the centre of a small grey area, an eye-spot was placed consisting of a black centre surrounded by a white ring, the proportion of black to white being so arranged that, after blending, they were equal in tone to the surrounding grey; a similar grey area was prepared but with no central eye-spot: these two squares were then examined against various backgrounds; at the same time the squares were gradually reduced in size: it was then found that when the square (text-fig. 3, *11*) was reduced to 12·75 mm., the edges began to be blurred as compared with the edges of text-fig. 3, *12*, especially against backgrounds not widely different in tone. Further reduction of the square to 10·3 mm. heightened the difference.

In this particular experiment the size of the eye-spot was: total diameter 6·75 mm., black centre diameter 4 mm. Eye-spots of different diameters were also used, and it was found that the larger the spot, the greater the distance at which marginal blurring was produced. Some experiments were also made, in which the eye-spots were drawn so that after blending they were different in tone from the surrounding grey. It was found that they were not very effective in margin-obscuring unless the background was closely similar to their tone, after blending: they appeared as either light or dark areas on the grey square. An experiment was next devised to discover whether this outline-blending, by means of an eye-spot, was more effective than other patterns. As shown in text-fig. 3, *13*, a grey square was prepared, in one corner of which a square eye-spot was placed, in another corner a square of the same size and containing the same proportion of black and white but distributed on either side of the diagonal, in a third angle a similar square divided down the middle, the fourth angle was left unoccupied. This square was then examined against various backgrounds. Two facts were recorded: first, the eye-spot blended at a much shorter distance than the other two black and white squares, and secondly, the eye-spot square more effectively blurred the angle of the grey square than did the other two patterns. It was, however, difficult to decide how much difference there really was, because at the distance at which the eye-spot was blended and producing blending at the corner of the square, the other two patterns had not blended. In order to show the differences in the blending distance: under the conditions of the experiment, the blending distances of these patterns (text-fig. 3, *14–16*) were as follows: eye-spot $18\frac{1}{2}$ feet, diagonally divided square $32\frac{1}{2}$ feet, medially divided square 35 feet. Eye-spots distributed over a surface are often used for producing a pattern; in Lepidoptera they often form marginal patterns, but more frequently form patterns some distance from the edge, as is also the case in the Jaguar (see text-fig. 3, *17*).

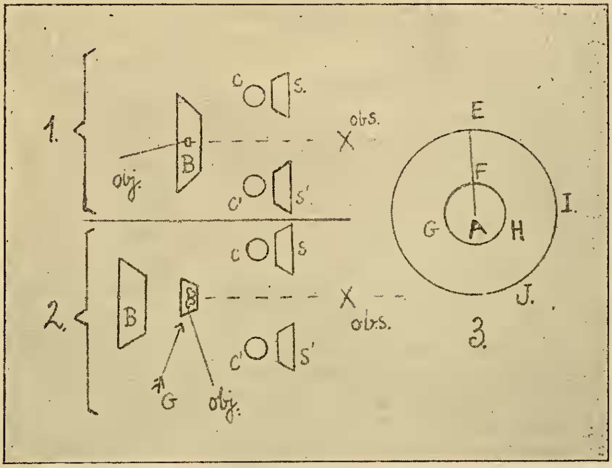
It appears that a given quantity of black and white, used as circular eye-spots, forms a pattern which obscures the outline, if not better, at any rate as well as other patterns. In order to be effective in this respect the eye-spot, after blending, should not make a contrast in tone with its ground; this was found to be the case as regards the eye-spots on the under wings of a number of butterflies examined: for instance, when the groundwork was light, the dark in the eye-spot was either small or not deep in tone.

Other possible uses for eye-spots have been put forward: they have been thought to be attraction marks which induce the attacking enemy to strike them rather than vulnerable parts; they have been looked upon as "dazzlers" to divert the enemy's eye from the insect as a whole. If one examines the larger eye-spots and those on the dorsal surface of the wings of many butterflies, one finds that they do not, after blending, harmonise with the rest of the wing; thus it would appear that they probably have a different function from those found on the under wings, which it has been thought are for concealment.

Patterns have been considered as regards their powers of concealing form, against plain backgrounds only. Against mottled backgrounds, which probably are more common in nature, these powers of concealment are as effective, not because they may copy or be paintings of anything in the background (they may be), but because after blending they will cause the animal to fade into its surroundings.

Beyond the blending distance of a pattern, the question as to whether the pattern does or does not imitate some part of the animal's surroundings, does not come in: pattern can only be effective in concealing form by means of mimicry or protective coloration, within its blending distance; nevertheless, beyond blending distance, as has been seen, pattern still has powers of concealing form. It is possible that a given pattern may combine both these uses. Suppose AE (text-fig. 5, *3*) be the extreme

Text-figure 5.



1. Ground plan of apparatus for experiments with artificial patterns.

2. The same, modified for measuring the blending distance of the patterns of insects' wings.

Notes referring to 1 and 2.

B=backgrounds made of 'Velox' paper exposed for varying lengths of time.

C & C′=standard candles.

S & S′=screens of "Bristol" board painted black.

obj.=object to be examined.

G=glass plate on which is glued a small bead of cork to which the insect is pinned.

obs.=observer along the dotted line.

Using the following distances, an illumination is obtained not unlike that under a hedge on a dull day:—

C–S and C′–S′= 6 cm.
C–obj. and C′–obj.=40 cm.
C–C′=40 cm.
G–B=20 cm.

distance at which animal A is visible, and AF be the distance at which the pattern blends, then within the circle FGH the animal will be protected from enemies by mimicking its surroundings, and within the ring defined by FGH and EIJ by means of protective pattern-blending. The relative importance of these two methods of concealment will be according to the likelihood of enemies finding their way into the two areas, and the chance will be as the relative size of the two areas: the central area will, however, be at a somewhat greater disadvantage, because the enemy in arriving there, must pass through the outer area, and in so doing may discover its prey befoıe reaching the centre. The relative importance will also depend upon the eyesight of the enemy and the distance at which it commonly looks for its prey; those who have watched birds feeding upon insects have often remarked the long distances at which they can see their quarry. In order to illustrate the distance at which the patterns of insects blend, measurements were made in the case of sixteen insects, as shown in the following table.

It is obvious that the size of an animal must affect the size of its pattern: for instance, a pattern which blends at a few feet would be useless to an animal the size of the zebra. It appears, therefore, that it is necessary, whilst giving the blending distance of a pattern, to also state the size of the animal, and the relation of these two in the form of a ratio as is done in the table. Whether by comparing these pattern-blending ratios or indices, it is possible to separate animals presenting conspicuous patterns from those presenting inconspicuous ones, is beyond the scope of this paper. In the case of the insects examined, in some cases the dorsal surfaces of the wings have a high index, whereas the ventral aspects of the lower wings have all low indices, with the exception of the Queen of Spain Fritillary (*A. lathonia*). In this insect the high figure is probably due to the reflection of the candle-light from the "mirror" spots on the wing. It has been noted that the larger the pattern, the more effective the outline blending; on the other hand, the greater the blending distance of the pattern, probably the more conspicuous the animal: other things being equal, it follows, therefore, that a pattern may be so adjusted that the danger of it, short of blending, is counterbalanced by its concealing powers after blending. Finally, attention must be directed to one other aspect of these experiments. Deductions have been drawn from experiments carried out with the human eye: thus it is entirely a matter of opinion whether they would apply in the case of the eyes of animals. It is known that many animals are short-sighted compared with man, for instance, those of short stature and which for this reason have a near horizon: it may be that the lion at night cannot see the zebra's stripes until within close range. On the other hand, there is some evidence that in the case of certain birds, such as falcons, vision is more piercing than in man.

However, these deductions from experiments with the human eye are illustrated in the markings of animals' coats.

	Blending distance of pattern in cm.		Area of wings in sq. cm.		Index.	
	Dorsal surface of wings. A.	Ventral surface of posterior wings. B.	Of dorsal surface of wings. C.	Of ventral surface of posterior wings. D.	A./C.	B./D.
Small Copper (*Chrysophanus phlœas*)	680	50	1·5	0·8	453	62
Clouded Yellow (*Colias edusa*) ♂	1260	180	4·8	2·9	262	62
" " " " ♀	1230	180	4·8	2·9	256	62
Orange Tip (*Euchloë cardamines*) ♂	650	280	3·5	1·8	186	155
" " " " ♀	620	280	3·5	1·8	177	155
Swallow-tail (*Papilio machaon*)	1250	550	9·0	4·8	139	115
Red Admiral (*Pyrameis atalanta*)	880	520	6·4	3·7	137	141
Marbled White (*Melanargia galathea*)	640	360	4·8	2·9	133	123
Pearl-bordered Fritillary (*Argynnis euphrosyne*)	310	230	2·7	1·6	115	144
Speckled Wood (*Pyrarga egeria*)	390	360	3·5	2·1	111	171
Marsh Fritillary (*Melitæa aurinia*)	240	140	2·3	1·4	104	100
Small Tortoiseshell (*Vanessa urticæ*)	480	430	4·8	3·1	100	139
Large Tortoiseshell (*V. polychloros*)	680	380	6·8	3·5	100	109
Queen of Spain Fritillary (*A. lathonia*)	300	420	3·7	1·6	81	262
Grayling (*Satyrus semele*)	400	220	5·8	3·5	70	63
Silver-washed Fritillary (*A. paphia*)	310	230	7·2	4·0	50	77

NOTE:—The Blending distances were measured under the experimental conditions illustrated in text-fig. 5, *2*.

The Areas of the wings were estimated by the method of tracing on squared paper.

For comparison: checkered surface of black and white squares of 4 sq. mm. blended at 440 cm.

Conclusions.

(1) Obliterative shading in animals is sometimes effected by means of pattern-blending.

(2) The outlines of animals are frequently masked by the blending of patterns at or near their margins.

(3) Patterns having these effects are usually unlike the animal's surroundings and therefore cannot be of use in concealment by means of mimicry (using mimicry in the broadest sense of the word).